

**STUDIES OF SEED GERMINATION AND SEEDLING COMPETITION IN
VIRGILIA OROBOIDES (BERG.) SALTER, *ALBIZIA LOPHANTHA* (WILLD.)
BENTH. AND *ACACIA LONGIFOLIA* (ANDR.) WILLD.**

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ABSTRACT

A pilot ecological study comparing the indigenous legume tree *Virgilia oroboides* with two ecologically similar aliens, *Albizia lophantha* and *Acacia longifolia*, was initiated. Similarities were found in seed germination biology, with all three species showing rapid germination once seed dormancy is broken. Differential inhibition of seed germination with leaf litter and inter-specific seed-mix treatments was investigated and showed increasing sensitivity in the order *Virgilia*, *Albizia*, *Acacia*. A semi-natural replacement series interspecific seedling competition experiment revealed that all three species occupy similar niches. The order of aggressiveness was found to be *Virgilia*, *Albizia* then *Acacia*, the interaction effects being most clearly observed in the root biomass. Species seed-mass and energy-content were compared. Shoot and root increments relative to final shoot and root biomasses were also examined, in addition to the performance of each species in nutrient and non-nutrient media. All findings, together with further sundry observations, including *in vivo* seed and seedling predation measurements, were incorporated into the competition situation. Conclusions were that success of a particular species in a given combination of species depends on a large number of factors, e.g. varying nutrient and moisture availabilities of different soils, as well as differential predation on species. It is suggested that if the environment is manipulated correctly *Virgilia* (or other suitable indigenous species) could possibly be used as a subsidiary control measure against the invasive aliens *Albizia* and *Acacia*.

UITTREKSEL

STUDIES IN SAAD ONTKIEMING EN SAAILING KOMPETISIE BY *VIRGILIA OROBOIDES* (BERG.) SALTER, *ALBIZIA LOPHANTHA* (WILLD.) BENTH. EN *ACACIA LONGIFOLIA* (ANDR.) WILLD.

'n Loods ekologiese ondersoek om die inheemse peulplant boom *Virgilia oroboides* te vergelyk met twee ekologiese vergelykbare uitheemses, *Albizia lophantha* en *Acacia longifolia* is begin. Ooreenkomste met die saad ontkiemingsbiologie, waar al drie vinnig ontkiem na die verbreking van die rus. Differensiase met die onderdrukking van saad ontkieming met die blare met tussensoorte mengels wat ondersoek is, dui op 'n toename in sensitiviteit in die volgorde *Virgilia*, *Albizia*, *Acacia*. 'n Half-natuurlike vervangings reeks intersoort-kompetisie proef dui daarop dat al drie in vergelykbare posisies groei. Die volgorde van aggressieweïteit wat gevind is was *Virgilia*, *Albizia* en *Acacia* waar die interaksie effek die duidelikste uit die wortelbiomassa blyk. Loot en wortelgroei relatief tot die finale loot en wortelbiomassa was ondersoek en die groei van elke soort in 'n voedings en voedingslose media vergelyk. Alle bevindings, saam met verdere opmerkings insluitende *in vivo* saad en kiemplant benuttig meetings, word saamgevoeg in die kompeti-

sie situasie. Gevolgtrekkings dat die sukses van 'n bepaalde soort in 'n gegewe kombinasie van soorte afhang van 'n groot aantal faktore soos wisselende voedings en vogtigheid beskikbaarheid in verskillende gronde sowel as gedifferensieerde vreet op die soorte. Dit word voorgestel dat as die omgewing reg manipuleer word *Virgilia* (of 'n ander geskikte inheemse soort) moontlik gebruik kan word as 'n bykomende beheer maatreël teen die uitheemse *Albizia* en *Acacia* wat natuurlike veld inneem.

INTRODUCTION

Both *Albizia lophantha* and *Acacia longifolia* are invasive woody plants of Australian origin in the south-western Cape (Stirton, 1978). *Virgilia oroboides*, a southern and south-western Cape endemic (Coates Palgrave, 1977), is probably the nearest indigenous ecological analog of *A. lophantha* and *A. longifolia*. All three species occupy very similar habitats and have similar characteristics as indicated below:

1. All grow on moist, relatively fertile, south- and east-facing mountain slopes with similar altitudinal ranges.
2. All are nodulated legumes.
3. All are seed-regenerating species that grow from long-lived, hard-coated, pyrophytic seed which accumulate in the soil. None of the species coppice after fire.
4. Unlike most indigenous trees *Virgilia* has a very fast growth rate of up to 2 to 3 m per annum (Phillips, 1926), which is comparable with the rapid growth rates of the two introduced species.

Thus the broad hypothesis that *Virgilia* could, if environmental conditions were manipulated correctly, be given a competitive advantage over one or both of the two invasive Australian plants, was proposed and a pilot experimental study emphasizing interspecific interaction between all three species was conducted. The specific aims of the study were:

1. To compare the germination rates and percentages of each species (germinated alone), with the rates achieved on intra- and interspecific leaf litter mixtures, and in interspecific seed mixtures.
2. To compare energy contents of seeds of each species and to correlate the results with short-term, controlled interspecific seedling competition experiments.
3. To compare the rates of seedling shoot and root growth between species in soil, and in vermiculite with and without nutrients.
4. To make observations on the relative seed and seedling predation for each species in nature.

Seed and leaf-litter for these studies was collected in early summer of 1979 from Constantia Nek, Cape Province.

MAXIMUM SEED GERMINATION RATES

Seed germination tests

It has been demonstrated that poor germination responses in the three species are due principally to the impermeability of the testa to water (Phillips, 1926; Clements *et al.*, 1977). So all seeds were individually chipped at their micropylar ends to ensure the fastest possible germination response.

To investigate interspecific effects three replicate batches consisting of 50 seeds for each species, and in 1:1 ratios with each other, were placed in 50 mm petri dishes containing two No. 1 Whatman filter papers.

In the "leaf-litter" treatments the filter papers were inserted between 4 g of freshly ground leaf litter and the seeds. In order to prevent fungal infection the procedure given by Clemens *et al.* (1977) was followed.

All germination and incubation experiments were conducted at 27 °C (± 1 °C). Relative humidity was controlled at 100 %, and daylength adjusted to a constant 12-hour period at an intensity of 40 000 lux. Adequate moisture conditions were maintained in each dish and counts of germinated seeds (i.e. seed with emerged radicle length greater than 1 mm) were made daily over a period of 14 days. Germinated seeds were not removed for the duration of the test period.

The mean daily percentage germinations were arc-sine transformed to make them suitable for the analysis of variance (Sokal and Rohlf, 1969). Initially both the rates and final germination percentages for pure seeds of each species were compared with one another visually at the 95 % confidence limit. The number of days taken for half the sample to germinate (mean day) was also calculated for each species, together with the standard deviation. Separate comparisons were then made between the arc-sine transformed data for daily germination of pure seeds, seeds on litter, and seed-mixes for each species. As the daily germination rates of the treated seeds and the standards (pure seeds) were compared individually, a series of standard *t* tests was applied to determine whether the differences were significant.

Results

Germination was quick and decisive with no changes in percentage germination beyond day five. The germination rates of standards were similar for all species (Figure 1). The time taken for half the seeds of each species to germinate was 0.8; 0.8 and 1.5 days for *Virgilia*, *Albizia* and *Acacia* respectively.

Discussion

Virgilia seeds showed relatively low inhibition of germination in all treatments (Figure 2a). Only on the first and second days on *Albizia* litter, and on the first day on *Acacia* litter, was there a significant reduction of germination rate compared with the pure seed standard (Table 1).

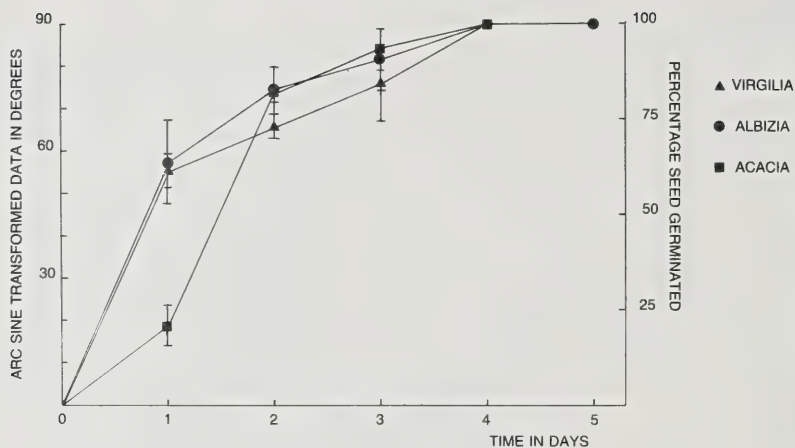


FIG. 1.
Germination rates of seeds (95 % confidence limits shown)

Albizia seeds showed greater sensitivity than *Virgilia* seeds to the leaf litter and seed-mix treatments (Figure 2b). Inhibition of germination was most pronounced with the leaf-litter treatments, being greatest on its own and on *Virgilia* litter, and showing significant inhibition from day 3 onwards on *Acacia* litter. The actual rates of germination were significantly reduced in the seed-mix treatments only from day 1 to day 3 with *Virgilia* seeds, and only for day 1 with *Acacia* seeds (Table 1).

Of all the species *Acacia* exhibited greatest inhibition. With the exception of the *Albizia* mix all other treatments produced marked inhibition of both the rates, and the overall final germination of the *Acacia* seed (Figure 2c, Table 1).

Of interest was the fact that the litter of the parent species caused greater inhibition to the germination of both *Acacia* and *Albizia* and appeared insignificant in *Virgilia* (Figures 2a, b, c, Table 1).

SEEDLING COMPETITION STUDIES

Assessment of seed mass, energy content and moisture content

Fifty seeds of each species were each weighed then dehydrated whole at 65°C for seven days and re-weighed. These seeds were then finely ground and dehydrated for a further three days and re-weighed again. It was, therefore, possible to compare resistance of each species to dehydration through the seed-coat with its overall moisture content. The calorific value of 2 g sub-samples of each dried sample was then obtained by means of bomb calorimetry.

TABLE 1.
Germination rates in days of treated seeds compared with pure standards - t values ($t^{0.05} = 2.776$).

Treatment	VIRGILIA				ALBIZIA				ACACIA			
	1	2	3	4	1	2	3	4	1	2	3	4
On VIRGILIA litter	1.01	0.03	0.20	2.02	[>5	>5	>5	>5	[3.05	>5	>5	>5
On ALBIZIA litter	[>5	>5	2.34	1.76	[>5	>5	>5	>5	[>5	>5	>5	>5
On ACACIA litter	[4.63	2.69	1.58	1.93	[>5	2.16	3.40	>5	[2.79	>5	>5	>5
With VIRGILIA seeds	—	—	—	—	[3.57	2.83	2.90	1.38	[>5	>5	>5	5.34
With ALBIZIA seeds	1.85	0.75	0.36	2.02	—	—	—	—	1.52	0.26	0.20	—
With ACACIA seeds	1.47	3.65	0.34	2.01	[3.39	0.12	0.32	0.30	—	—	—	—

[] Indicates period of inhibition

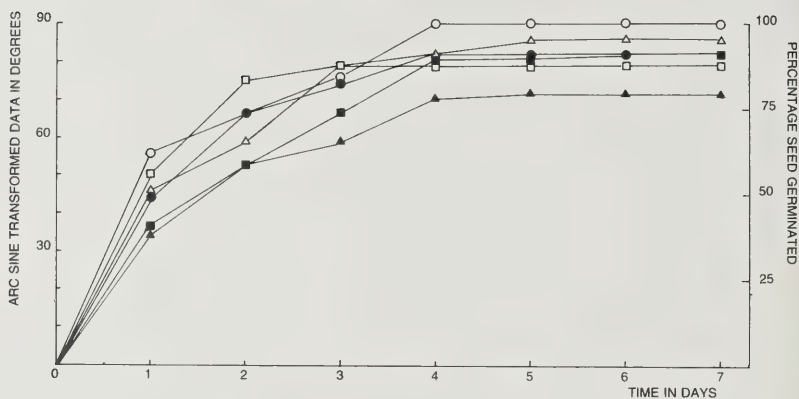


FIG. 2a.
Germination rates of *Virginia*.

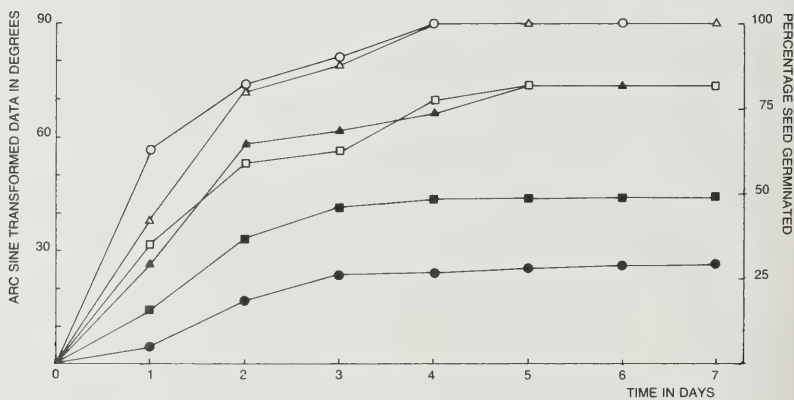


FIG. 2b.
Germination rates of *Albizia*.

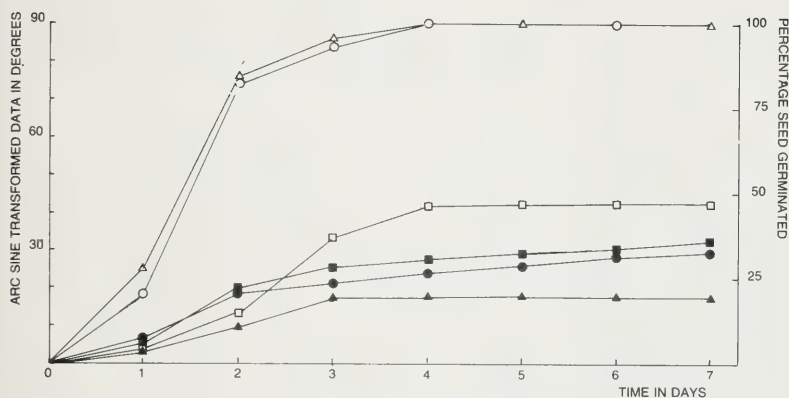


FIG. 2c.
Germination rates of *Acacia*.

Key to Fig. 2a, b, c

- Species I (J, K) plain.
- △ Species I (J, K) with seeds of species J (K, I)
- Species I (J, K) with seeds of species K (I, J)
- Species I (J, K) on litter of species I (J, K)
- ▲ Species I (J, K) on litter of species J (K, L)
- Species I (J, K) on litter of species K (I, J)
- I = *Virgilia oroboides*
- J = *Albizia lophantha*
- K = *Acacia longifolia*

Discussion

The individual seed weights showed a very low standard deviation; *Albizia* produced the heaviest seeds, followed closely by *Virgilia*, with *Acacia* having the lightest seeds.

A modified *t* test for small sample size, the Lord's Range test (Sokal and Rohlf, 1969) showed that individual seed energies were significantly different at $L^{0.05}$ for *Albizia* and *Virgilia*, and also at $L^{0.01}$ for *Acacia* compared with *Virgilia* and for *Acacia* compared with *Albizia*. The seed energy/undried seed mass ratios showed the same order of magnitude as the individual undried seed mass. However, the ratio for *Acacia* was lower than that of both the other species. This means that, relative to the other species, even less energy is present in the *Acacia* seed than is apparent from the undried mass.

TABLE 2.
Comparison between seed mass, seed moisture content and seed energy content for *Virgilia*, *Albizia*, and *Acacia*
($L\ 0.05 = 1.71/L\ 0.01 = 3.96$)

Species	Mass of seed 9	Percentage moisture loss after whole seed desicca- tion at 65 °C for 7 days	Total percentages moisture	Sub-sample batch number for energy determina- tion	Energy per gram of dried seed KJ	Energy per gram of un- dried seed KJ	Energy per seed KJ	L values between species for seed energies
<i>VIRGILIA</i>	0.07858 ± 0.00004	91.31	7.02	1 2 Mean	21.283 21.861 21.572		1.5550 1.5972 1.5761	<i>VIRGILIA</i> vs. <i>ALBIZIA</i> 1.772
<i>ALBIZIA</i>	0.09255 ± 0.00005	67.61	7.75	1 2 Mean	20.650 21.682 21.166		1.7630 1.8511 1.8078	<i>ALBIZIA</i> vs. <i>ACACIA</i> 16.449
<i>ACACIA</i>	0.016650 ± 0.000007	62.22	8.92	1 2 Mean	18.008 18.341 18.175		0.2731 0.2781 0.2756	<i>ACACIA</i> vs. <i>VIRGILIA</i> 27.553

Of all the test species *Virgilia*, when dehydrated whole, showed the highest percentage of overall moisture content lost through its seed-coat. This presumably indicates a higher seed-coat permeability.

Seedling competition using the replacement series technique

Freshly germinated seed of *Virgilia*, *Albizia* and *Acacia* were sown in pure cultures, as well as in 1:1 mixtures with species individuals set alternately to one another. Fallen seed of *Virgilia* may be found in natural concentrations of up to 0.2 seeds per cm² (Phillips, 1926), whereas that of *Acacia* can be found at concentrations of up to 3 seeds per cm² (Milton, 1980). Germinated seed were set at concentrations of 1 per cm² in 7 × 7 matrices (with the omission of plantings at the 49th position, allowing equal numbers per species). Two replicate matrices were prepared for both pure and mixed cultures. The rich loam soil used for the experiment was taken from the A horizon at a site in the Kirstenbosch National Botanic Gardens, where all three test species are known to grow vigorously.

The experiment was conducted outside during late autumn and winter, a cool wet period in the south-western Cape when natural germination in the field had been observed. Precautions were taken against predation, and a transparent (95 % light transmission) corrugated fibre-glass sheet was suspended 1 m above the seedling containers to permit controlled watering.

After twelve weeks the seedlings were harvested, cleaned and then dried at 80 °C. The total dry-mass measurements for shoot and root biomasses were taken separately for each species from each culture, and representative examples were photocopied for visual comparison (Figures 3b, 4b and 5b).

Analysis of data

The "replacement series" approach is an experimental design devised by de Wit (1960) to measure the effects of one species on the other in species combinations grown in mixtures. This approach adopts as a standard for comparison the pure stands of each species grown at the same densities as the mixtures, thus allowing all conclusions to be determined on a proportional and therefore relative basis. Results are represented pictorially by means of "replacement series" curves for each species combination. This procedure was followed with the data from the present experiment (Figures 3a, 4a and 5a).

In addition the data were analysed to determine certain important features concerning species interactions. In order to determine whether each test species possesses ecological niche overlap with the others (i.e. whether there is competition for common limiting resources), the "Relative Yield Totals" (RYT) for each of the interacting species pairs were calculated. The sum of the relative yields of species "I" grown in mixtures with species "J" (R_I) and of species J

grown in mixtures with species "I" (R_I) is equivalent to the RYT for the two species. Here

$$R_I = \frac{M_I}{P_I} \text{ and } R_J = \frac{M_J}{P_J}$$

where $M_{I(J)}$ = yield of species $I(J)$ in mixture, and $P_{I(J)}$ = yield of species $I(J)$ in a pure stand. If the RYT values are equal to unity this indicates that the mixed species pairs fill the identical ecological "space" (Harper, 1977). In order to determine the statistical significance of the conclusions inferred by the RYT values, the actual yield of each mixture was compared with the sum of half the actual yields of the two corresponding pure cultures, following the method of Burdon and Pryor (1975). The "Lord's Range test" was used to test whether the species in mixtures were occupying the same ecological niche.

Even if it is found that the species occupy sufficiently similar ecological niches to allow direct competition for resources, this factor gives no information about the significance of relative enhancement/inhibition effects produced by the mixing. Thus inferences drawn from the shapes of the "replacement series" curves (convexity illustrating enhancement and concavity inhibition) were tested. Lord's Range values were thus calculated to see whether the difference was significant between relative yields for the replicate pairs of each species and the corresponding pairs of "expected" relative yields. The "expected" relative yield is defined as being half the value of the calculated RYT for each replicate.

In order to extend the conclusions concerning the effects of the test species interactions, similar "relative yield" analyses were completed for both shoots and roots separately. Actual shoot-root yield borderlines were also depicted on the "replacement series" diagrams.

Results and discussion

All RYT values (which are marked on Figures 3a, 4a, 5a) were found to be close to unity, thus providing a rough indication that the test species fill very similar ecological niches to one another. Comparisons of the actual yields for each mixture with the sum of half the actual yields of the corresponding pure cultures produced values which were all insignificant at $L^{0.05}$. This means that one must accept the null hypothesis that the species are competing with one another for the same ecological space, which agrees with the conclusions obtained from the RYT values. Inspection of the L values (Table 3) gives an indication of the ecological relationships between the species as regards competition for the same resources. The order of increasing ecological "relatedness" appears to be as follows: *Virgilia-Acacia*, *Virgilia-Albizia* and lastly, *Albizia-Acacia*.

Species Pair	Yield mixed vs. Yield pure	Relative Yield Total (RYT)	Species	Total Plants RY vs. $\frac{1}{2}$ RYT	Shoots alone RY _s vs. $\frac{1}{2}$ RYT _p	Roots alone RY _r vs. $\frac{1}{2}$ RYT _p
<i>VIRGILIA</i> vs. <i>ALBIZIA</i>	1.3482	1.0583	<i>VIRGILIA</i>	1.1531	0.6014	5.6933 (S)
<i>ALBIZIA</i> vs. <i>ACACIA</i>	0.6306	1.0795	<i>ALBIZIA</i>	2.4430 (S)	1.0771	4.0856 (S)
<i>ACACIA</i> vs. <i>VIRGILIA</i>	1.5952	0.9882	<i>ACACIA</i>	2.3828 (S)	1.3713	5.3327 (S)
			<i>VIRGILIA</i>	0.8429	0.8429	2.3150 (S)

TABLE 3.
Competition between species and effects of interaction in mixture: *L* values ($L_{0.05} = 1.71$ and $L_{0.01} = 3.96$)

The replacement series curves indicate fairly marked enhancement/inhibition effects between the various competing species pairs (Figures 3a, 4a, 5a). The Lord's Range comparisons of the relative yields and $\frac{1}{2}$ RYT's revealed significance at the 95 % level for all competitors, with the exception of *Virgilia* (Table 3). However, it must be emphasized that both *Albizia* and *Acacia* show significant inhibition in biomass increment in the presence of *Virgilia*.

Finally, *Albizia* is significantly enhanced and *Acacia* significantly depressed when in mixture.

The comparisons between expected relative yield and observed relative yields, calculated for shoots and roots separately, show very definite differences between the respective *L* values (Table 3). It is clear that differences in the observed relative yields of *shoots* alone, for all the species pairs, is insignificant at the 95 % confidence level. That most competitive enhancement/inhibition effects are manifest in the root relative yields is clearly indicated by the much higher *L* values. Root relative yields show significant differences from the expected values for all species in all combinations with some *L* values even exceeding the 99 % confidence levels: *Virgilia* is enhanced when in mixture with *Albizia*; *Acacia* is inhibited when in mixture with *Virgilia* and *Albizia* is enhanced when in mixture with *Acacia*. Some of the general competition effects for each species are apparent in Figures 3b, 4b and 5b.

In summary, the test species appear to occupy very similar niches with competition being, therefore, direct, and with the interaction effects being most significant in the roots.

EARLY SHOOT AND ROOT GROWTH RATES

A comparison between the shoot and root growth rates of seedlings in soil

Seedlings of *Virgilia*, *Albizia* and *Acacia* were grown in specially constructed root chambers (Gerard, 1978), set at 45° to the vertical, and root elongation was recorded at fortnightly intervals. The soil used and the environmental conditions for growth were the same as those employed in the seedling competition experiment. Marked root growth increments were later measured by means of an opisometer.

Simultaneously with the recording of root increments measurements of shoot heights were also taken for each plant.

At the end of 9 weeks the seedlings were harvested, cleaned and photographed in order to determine approximately what proportion of the roots had been visible through the transparent perspex sides of the chambers while growth was being monitored. Finally the seedlings were oven dried at 80°C and weighed.

Results and discussion

Cumulative shoot and root increments were compared between species for

RYT for 0.5/0.5 mixture = 1.056

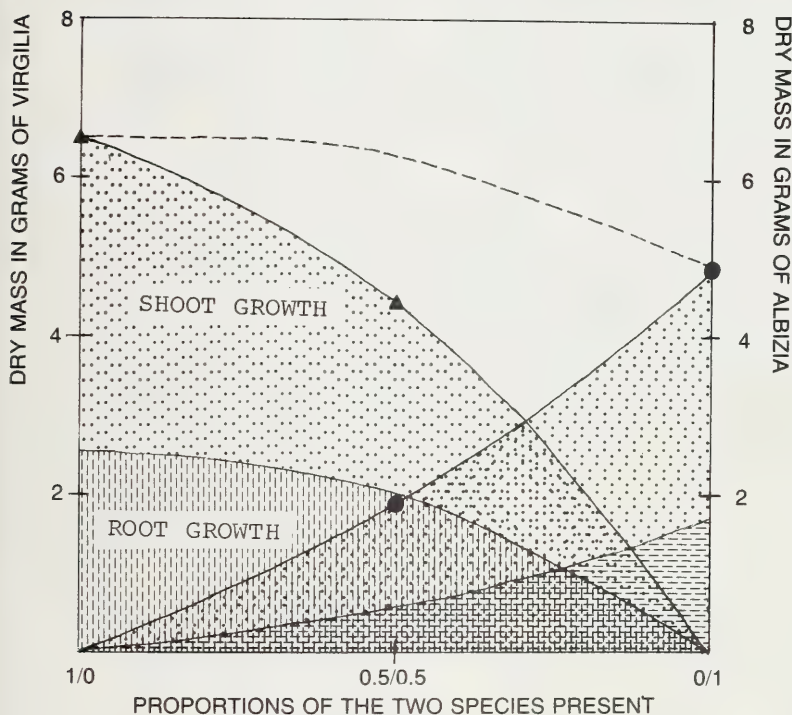


FIG. 3a.

A "replacement" series diagram of *Virgilia* = ▲ vs. *Albizia* = ●.

each time interval using a series of one-way Anova variance tests (Sokal and Rohlf, 1969). If the null hypothesis for these tests was rejected the Tukey's method of multiple comparisons (Zar, 1974) was applied to test significance between individual species combinations. It was thus possible to determine if and when seedlings of each species showed significantly different root and shoot growth rates from one another. A similar analysis was also performed to test differences between the final mean dry weights for each species.



FIG. 3b.

Seedlings selected at random from pure and mixed stands by *Virgilia*, *Albizia*—showing effects of interaction.

- (a) 'Pure' *Virgilia* (b) 'Mixed' *Virgilia*—slightly enhanced root development
 (c) 'Pure' *Albizia* (d) 'Mixed' *Albizia*—slightly reduced root development

RYT for 0.5/0.5 mixture = 1.082

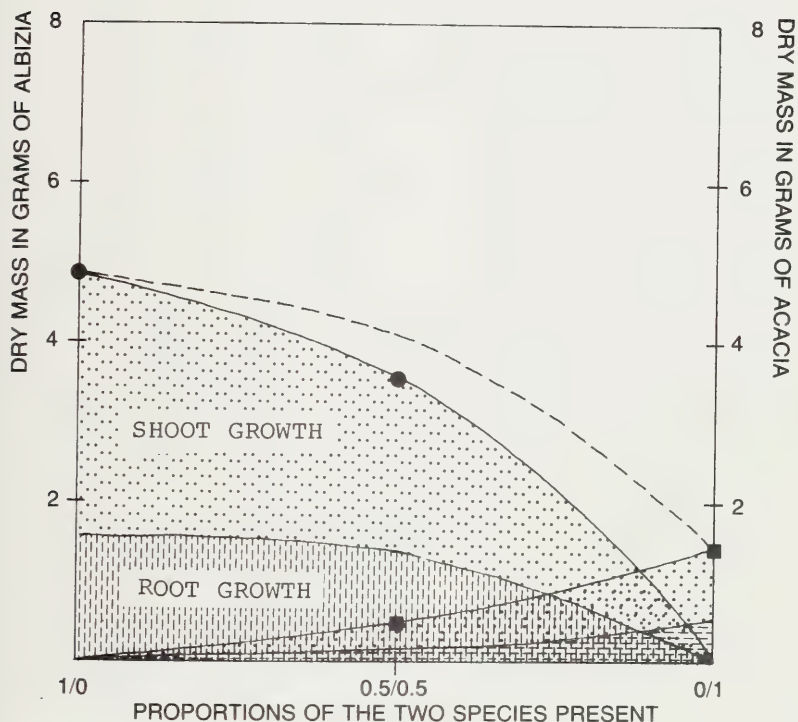


FIG. 4a.

A "replacement" series diagram of *Albizia* = ● vs. *Acacia* = ■.

In addition, certain proportions, together with standard deviations, concerning shoots and roots, were calculated and comparisons made. These were, firstly, final root/shoot length and root/shoot dry-weight proportions and secondly, final shoot weight/shoot length and root weight/root length proportions.

Visual comparison between the photocopied seedling roots (Figure 6c) and the transparent sheets whereon root growth increments had been traced, showed that a considerable part of the root length had been visible during the monitoring procedure.



FIG. 4b

Seedlings selected at random from pure and mixed stands of *Albizia*, *Acacia*—showing effects of interaction.

- (a) 'Pure' *Albizia*
- (b) 'Mixed' *Albizia*—slightly enhanced root development
- (c) 'Pure' *Acacia*
- (d) 'Mixed' *Acacia*—reduced root development and etiolated stems and leaves

RYT for 0.5/0.5 mixture = 0.986

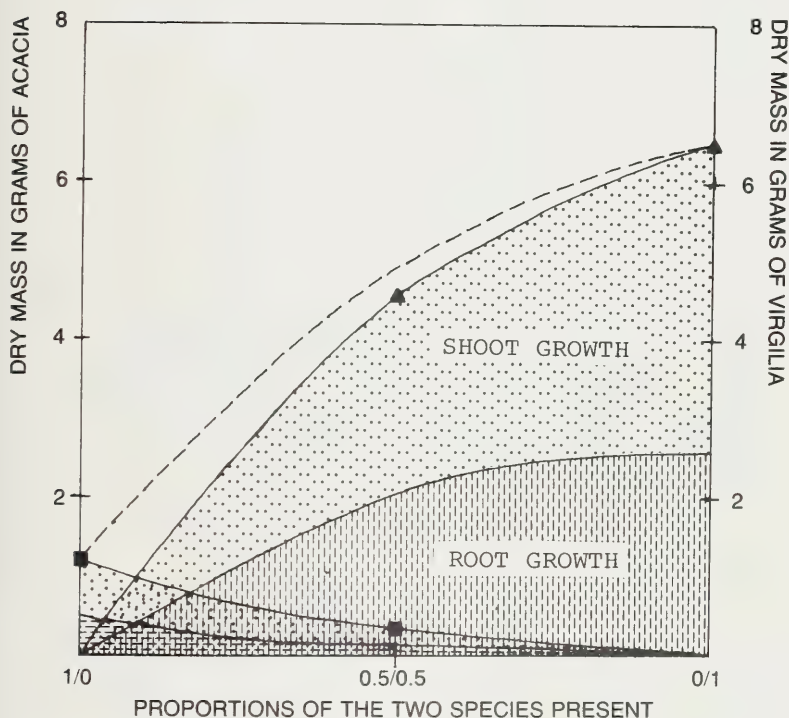


FIG. 5a.

A "replacement" series diagram of *Acacia* = ■ vs. *Virgilia* = ▲.

The comparison of rates of shoot increment showed significant differences between species throughout (Table 4a). From the curves in Figure 6a it can be noted that the rates of growth for all species appear most rapid over the first two weeks, probably as a result of the initial seed energy content. Although *Virgilia* shows a significantly greater shoot length increment than *Albizia* from week 4 onwards, *Albizia* appears to possess a slightly faster rate of growth than *Virgilia*, possibly indicating that the former could eventually out-compete the latter. A

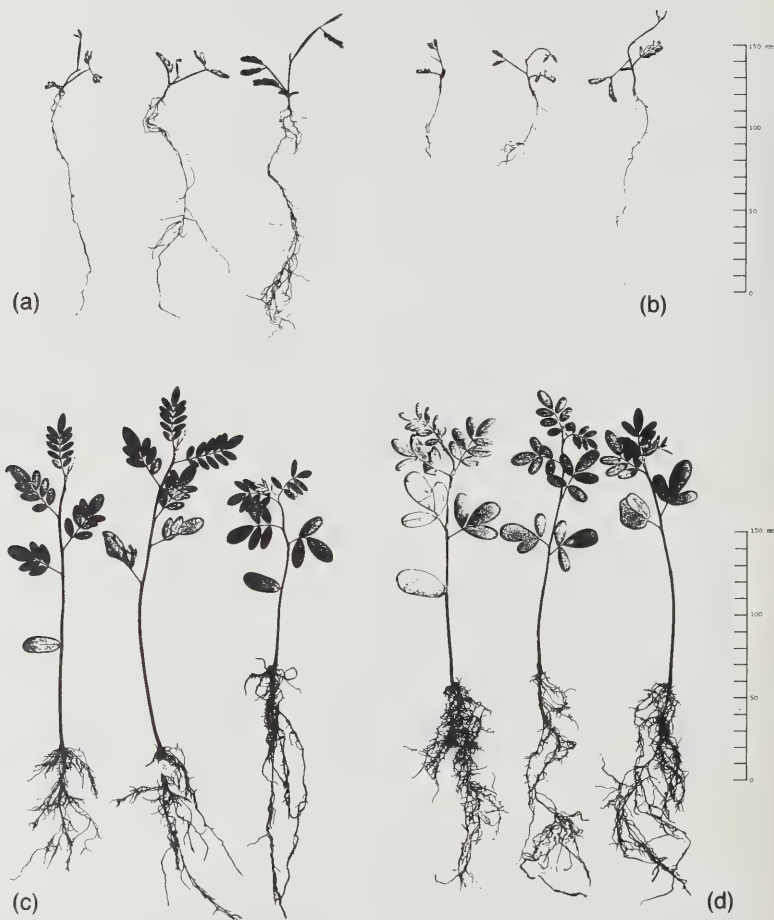


FIG. 5b.

Seedlings selected at random from pure and mixed stands of *Acacia*, *Virgilia*—showing effects of interaction.

- (a) 'Pure' *Acacia*
- (b) 'Mixed' *Acacia*—reduced root development and etiolated stems and leaves
- (c) 'Pure' *Virgilia*
- (d) 'Mixed' *Virgilia*—enhanced root development

TABLE 4a.
(ii) Tukey's Range Values = 0.05
[If confidence interval does not include 0—reject $H_0 = (S)$]

		Number of Weeks			
		2	4	6	9
Shoots	μ_{vi} vs. μ_{al}	0.84 → 3.36 (S)	0.02 → 3.76 (S)	0.30 → 3.70 (S)	0.44 → 3.76 (S)
	μ_{al} vs. μ_{ac}	0.31 → 2.83 (S)	0.51 → 4.29 (S)	1.27 → 4.67 (S)	2.02 → 5.34 (S)
	μ_{ac} vs. μ_{vi}	2.41 → 4.93 (S)	2.38 → 6.16 (S)	3.27 → 6.67 (S)	4.12 → 7.44 (S)
Roots	μ_{vi} vs. μ_{al}	2.37 → 10.43 (S)	11.52 → 45.08 (S)	-0.86 → 112.66 (NS)	-65.31 → 148.51 (NS)
	μ_{al} vs. μ_{ac}	-2.63 → 5.43 (NS)	-12.38 → 21.18 (NS)	-35.06 → 78.46 (NS)	-32.31 → 181.51 (NS)
	μ_{ac} vs. μ_{vi}	3.77 → 11.83 (S)	15.90 → 49.48 (S)	20.84 → 134.46 (S)	9.29 → 223.11 (S)

μ_{vi} = Mean for *Virgilia*

μ_{al} = Mean for *Albizia*

μ_{ac} = Mean for *Acacia*

TABLE 4a.

Comparative rates of shoot and root growth in soil between all species: Anova *F* values and Tukey's ranges

(i) *F* observed values $F = 5.14$

	NUMBER OF WEEKS			
	2	4	6	9
Shoots	41.13	41.70	42.92	58.77
Roots	51.27	21.06	9.36	5.704

(Reject *H*₀ throughout)

TABLE 4b.

Comparative rates of shoot and root growth in soil between all species

(i) *Dry mass in soil and interspecific comparisons*

$F = 5.14$

Species	Total dry mass	Anova between species F_{OBS}	Tukey's confidence intervals [if not including 0 reject <i>H</i> ₀ (S)]
<i>VIRGILIA</i>	.2790	43.6	VIRG. vs. ALB. 0.09 → 0.26 (S)
<i>ALBIZIA</i>	.1018		ALB. vs. ACAC. -0.01 → 0.16 (NS)
<i>ACACIA</i>	.0250		ACAC. vs. VIRG. 0.17 → 0.34 (S)

(ii) Species Shoot/Root proportions (with standard deviations)

Species	$\frac{\text{Root length}}{\text{Shoot length}}$	$\frac{\text{Root weight}}{\text{Shoot weight}}$	$\frac{\text{Shoot weight}}{\text{Shoot length}}$	$\frac{\text{Root weight}}{\text{Root weight}}$
<i>VIRGILIA</i>	22.9 ± 6.2	2.71 ± 0.07	0.0118 ± 0.0010	0.00149 ± 0.00027
<i>ALBIZIA</i>	24.7 ± 3.3	0.873 ± 0.001	0.0132 ± 0.0009	0.00048 ± 0.00007
<i>ACACIA</i>	64.0 ± 21.2	0.68 ± 0.16	0.0305 ± 0.0124	0.00036 ± 0.00008

similar situation applies in the case of root growth in which *Albizia* ceases to show a significantly lower root length increment than *Virgilia* from week 6 onwards (Figure 6b, Table 4a).

Acacia differs from the other species with regard to relative shoot and root growth rates. The shoot length increment from week 2 to week 9 is virtually negligible, unlike the other species, whereas the root length increase is continuous, following a similar pattern to the others (Figures 6a and 6b).

The dry mass of the harvested plants showed no significance in difference between the means of *Albizia* and *Acacia* (Table 4b).

The proportions of root/shoot length increased in the following order: *Virgilia*, *Albizia*, followed by *Acacia* with the highest value (Table 4b). However, root/shoot dry-weight ratios showed the reverse trend.

Further inspection of the data in Table 4b shows that the shoot dry weight/shoot length values are in the approximate ratio of 15:17:38 for *Virgilia*, *Albizia*, *Acacia* respectively, indicating a significantly higher value for *Acacia*. However, the corresponding root dry weight/root length ratios, which are 15:5:4, show that *Virgilia* has the highest value for this parameter.

Thus it seems clear that both *Albizia* and *Acacia* produce greater lengths of root for less energy than *Virgilia*. Of less importance is the fact that *Virgilia* and *Albizia* allocate lower energy per length of stem than *Acacia*.

Finally some other general observations can be mentioned. *Albizia* shed its reddish-yellow embryonic seed cotyledons within the first three weeks after planting. The cotyledons of *Virgilia* and *Acacia*, on the other hand, turned green, hence photosynthetic, soon after germination and were retained for the full test period (Figure 6c). It was also noted that the *Acacia* seedlings did not develop phyllodes (characteristic of mature plants of this species) during the same period (Figure 6c). (In additional unharvested specimens these became apparent only at about 3 months of age).

COMPARATIVE ROOT AND SHOOT RATES FOR EACH SPECIES IN VERMICULITE WITH AND WITHOUT NUTRIENTS

The same experimental design and timing as described in the previous section were used for measuring root and shoot growth rates in this experiment. Instead of soil a Grade 3, coarse-grained vermiculite was used as a growth medium. Three replicate seedlings of each species and for each treatment were grown in two sets of nine root chambers.

To the first set of root chambers an application of 100 ml balanced nutrient solution was added to each seedling on a fortnightly basis for the full experimental nine week growth period. Concentrations of the nutrients added were as follows: $\text{Ca}(\text{NO}_3)_2 \cdot 4\text{H}_2\text{O} = 1.35 \text{ g/l}$, $\text{NaNO}_3 = 0.6737 \text{ g/l}$, $\text{NaH}_2\text{PO}_4 \cdot 2\text{H}_2\text{O} = 0.4188 \text{ g/l}$, $\text{Na}_2\text{HPO}_4 \cdot 12\text{H}_2\text{O} = 0.4727 \text{ g/l}$, $\text{K}_2\text{SO}_4 = 0.7500 \text{ g/l}$,

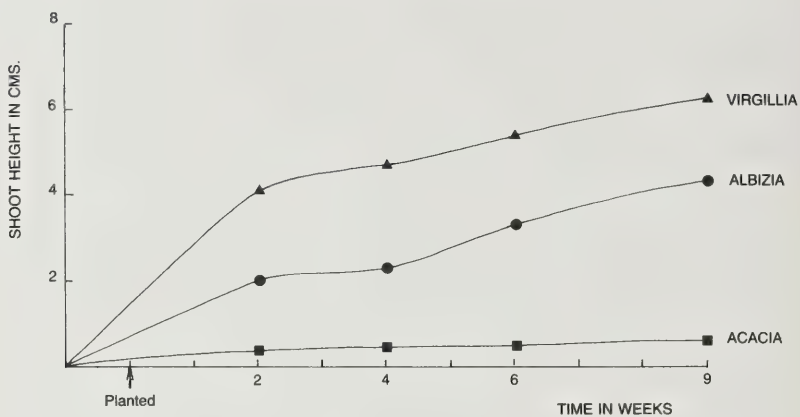


FIG. 6a.
Growth of shoots in root chambers.

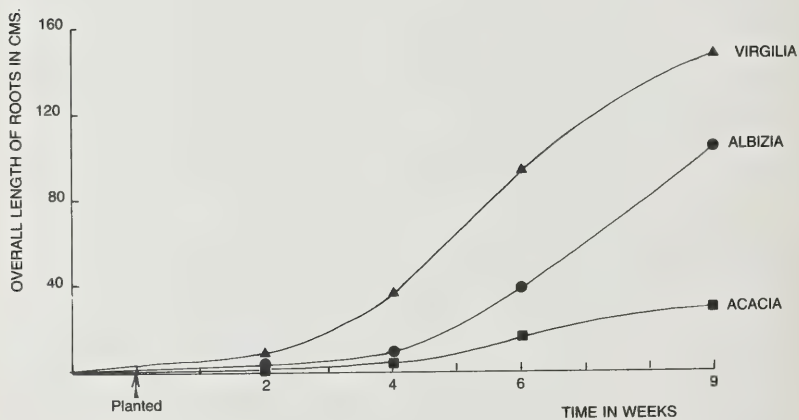


FIG. 6b.
Growth of roots in root chambers.



FIG. 6c.

Seedlings grown for nine weeks in root chambers in soil.

(a) *Virgilia*(b) *Albizia*(c) *Acacia*

$\text{Mg SO}_4 \cdot 7\text{H}_2\text{O} = 0,5500 \text{ g/l}$, $\text{Ca Cl}_2 \cdot 2\text{H}_2\text{O} = 0,285 \text{ g/l}$, $\text{FeNaEDTA} = 0,0300 \text{ g/l}$, $\text{H}_3 \text{BO}_3 = 0,858 \times 10^{-3} \text{ g/l}$, $\text{Mn Cl}_2 \cdot 4\text{H}_2\text{O} = 0,543 \times 10^{-3} \text{ g/l}$, $\text{Zn SO}_4 \cdot 7\text{H}_2\text{O} = 0,066 \times 10^{-3} \text{ g/l}$, $\text{Cu SO}_4 \cdot 5\text{H}_2\text{O} = 0,024 \times 10^{-3} \text{ g/l}$, $\text{H}_2\text{Mo O}_4 \cdot \text{H}_2\text{O} = 0,006 \times 10^{-3} \text{ g/l}$.

To the second seedling set no nutrients were added.

Results and discussion

Growth increments of shoots and roots were compared at each time interval for nutrient and non-nutrient treatments. In addition final dry weights for the seedlings were compared in the two treatments. Standard *t* tests were used to test significance throughout.

With the exception of root growth in *Albizia*, there were no significant differences between rates, or overall, shoot and root growths of any of the test species grown with or without the added nutrient solution (Table 5a, Figures 7a, b, c). With *Albizia* root growth was significantly reduced from week 6 to week 9 in the nutrient-treated plants, relative to the non-nutrient treated standards (Table 5a, Figure 7b).

Although the *Albizia* standards also showed a greater mean dry-weight than the nutrient-treated plants (Table 5b), this was not found to be significant (it may, however, imply a preference for very low nutrient levels). Similarly, no significance was found between mean dry weights for the separate treatments in *Virgilia* and *Acacia*, both of which showed lower *t* values than *Albizia* (Table 5b).

TABLE 5a.

Comparative rates of shoot growth in vermiculite, with and without added nutrients for each species: *t* values

Species		Number of weeks			
		2	4	6	9
<i>VIRGILIA</i>	Shoots	0.543 (NS)	0.660 (NS)	0.369 (NS)	0.168 (NS)
	Roots	0.095 (NS)	.045 (NS)	0.028 (NS)	0.082 (NS)
<i>ALBIZIA</i>	Shoots	0.823 (NS)	0.420 (NS)	0.530 (NS)	1.810 (NS)
	Roots	2.180 (NS)	2.400 (NS)	3.37 (S)	3.56 (S)
<i>ACACIA</i>	Shoots	1.797 (NS)	0.94 (NS)	1.200 (NS)	0.580 (NS)
	Roots	0.503 (NS)	2.160 (NS)	1.48 (NS)	0.58 (NS)

TABLE 5b.

Dry mass for each species with and without nutrients (*t* values compare effects of added nutrients)

Species	Treatment	Mean dry mass 9	<i>t</i> -Values
<i>VIRGILIA</i>	With nutrients	0.1952	0.395
	Without nutrients	0.1841	
<i>ALBIZIA</i>	With nutrients	0.1052	1.119
	Without nutrients	0.1372	
<i>ACACIA</i>	With nutrients	0.0176	0.626
	Without nutrients	0.0145	

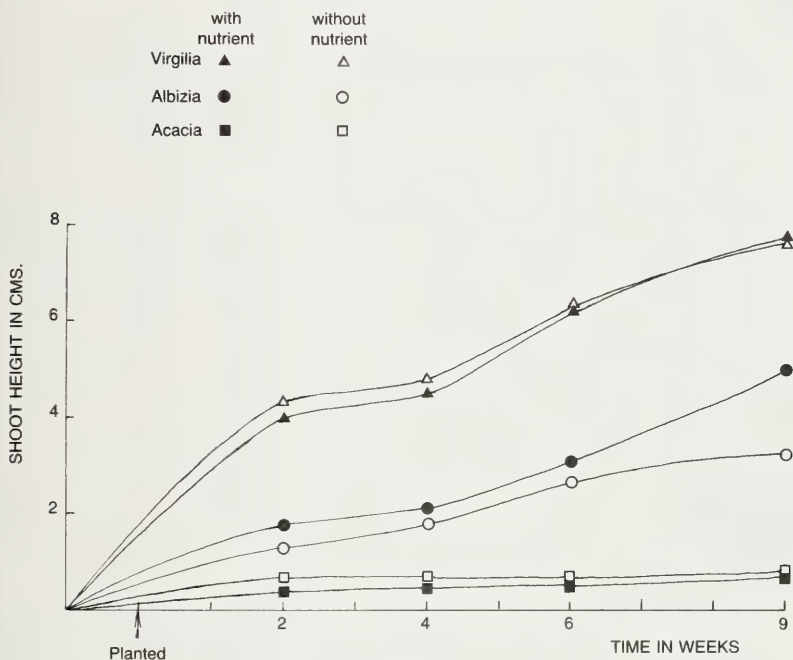


FIG. 7a.

Growth of shoots in nutrient and non-nutrient treated vermiculite in root chambers.

SOME MISCELLANEOUS OBSERVATIONS ON NATURAL SEED AND SEEDLING PREDATION AS WELL AS ON OVERALL SEED PRODUCTIVITY

In order to estimate whether differential seed predation may be a factor in reducing regeneration rates of any one of the test species, random samples of 50 seed pods were examined from trees of each species and the percentage of predated seeds was determined. In addition percentages of undeveloped, infertile seeds as well as the average numbers of seeds per pod for each species were measured.

Daily observations were also made on several seedlings of each species grown in the open during late autumn, to establish which species appeared most susceptible to seedling predation.

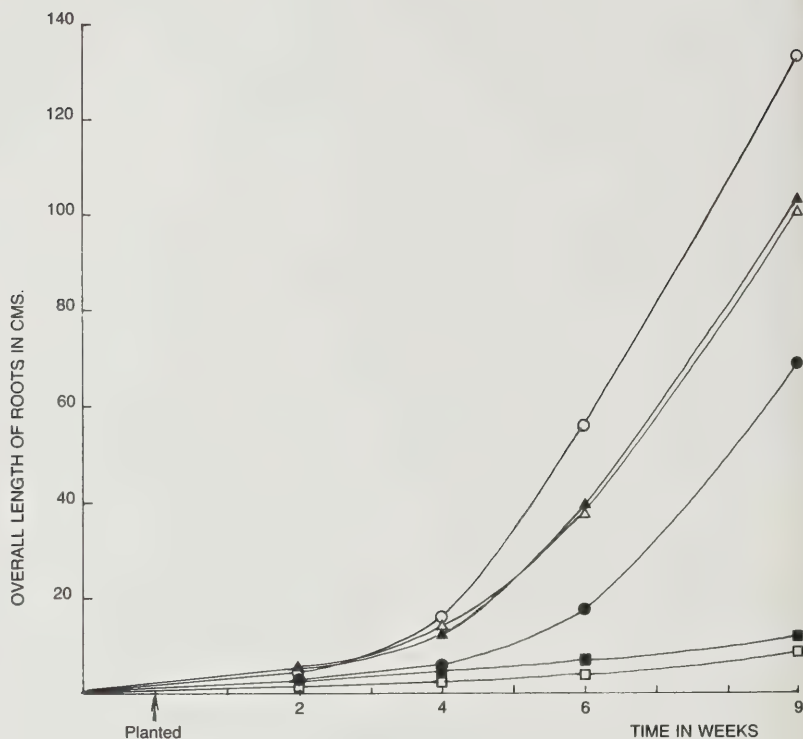


FIG. 7b.

Growth of roots in nutrient and non-nutrient treated vermiculite in root chambers.

Results

The average numbers of seed per pod and the percentages of seed found to be infertile are presented in Table 6. With single samples and fairly similar values between the species, it is difficult to draw definite conclusions from these two sets of data. However, it does seem valid to conclude that predation is higher in the seed of *Virgilia* than that of *Albizia* and *Acacia*: 9.68 % predated in *Virgilia* compared with 0 % in both *Albizia* and *Acacia* (Table 6). Moth larvae (undetermined species) are considered to be the chief *Virgilia* seed predators in the sample studied.



(i) Nutrient treated vermiculite



(ii) Non-nutrient treated vermiculite

FIG. 7c.

Seedlings grown for nine weeks in root chambers with nutrient and non-nutrient treated vermiculite.

(a) *Virgilia*

(b) *Albizia*

(c) *Acacia*

TABLE 6.

Numbers of seed per pod, and percentages of infertile and predated seed for random samples of fifty seed pods taken from single trees for each species.

Species	Average number of seeds per pod	Percentage of infertile seed	Percentage of seed predated
<i>VIRGILIA</i>	3.72	5.91	9.68
<i>ALBIZIA</i>	9.90	3.03	0.0
<i>ACACIA</i>	7.38	6.78	0.0

The daily observation of seedlings grown outside, unprotected from predators, revealed heavy nocturnal leaf-feeding activities by crickets on the *Virgilia* seedlings—in most cases leading to mortality within about a month of germination. In contrast, seedlings of *Albizia* and *Acacia* remained unaffected by the crickets, and also apparently, by any other forms of visible predation. The same cricket has been observed during the late autumn in the field beneath *Virgilia* leaf litter (at Constantia Nek).

GENERAL DISCUSSION

Chipping of seed at the micropylar ends produced an extremely rapid germination in all the species. The results are comparable with those produced by the most effective seed germination enhancing treatments obtained by Clemens *et al.* (1977) during germination tests on five Australian acacias (including *Acacia longifolia*).

The various germination inhibitions recorded with increasing sensitivity in the order: *Virgilia*, *Albizia*, *Acacia*, are difficult to explain either on a theoretical or functional basis. Theoretically, some form of allelopathic interaction, similar to that described for *Acacia cyclops* and *Acacia saligna* (= *A. cyanophylla*) by Jones *et al.* (1963), might be operative. However, much recent criticism of earlier attempts to prove the presence of allelotoxins experimentally (Harper, 1977) precludes any direct conclusions about the exact nature of the inhibitions recorded. Oily exudates with strong aromatic odour, similar to those recorded for *Casuarina littoralis* litter in the inhibition of *Eucalyptus ovata* germination (Withers, 1977), were also noticed in the moistened macerated litters of all three test species. It is possible that some indirect inhibiting effect, such as lowered oxygen availability produced as a result of litter decay may have been operating rather than an allelochemic reaction.

It does seem feasible that leaf litter and seed-mix inhibitions (whatever their exact cause) could operate in the field. The existence of auto-inhibition, or mortality of germinating seeds due to decaying litter beds, beneath dense stands of *Acacia* and *Albizia*, is supported by the observation that seed regeneration is absent in these situations. However, it is more likely that this suggested type of inhibition is subsidiary to that of the enforced dormancy produced by impermeable seed coats, although the dormancy could become broken down by seed-coat decay. The tests also revealed that *Acacia* and *Albizia* seed are inhibited by the litters of one another as well as by that of *Virgilia*. This lack of specificity of action may well imply that many other types of litter could be inhibitory. Trials with non-leguminous indigenous *Kiggelaria africana* litter appear to support this theory (McDowell, pers. obs.). It is of interest to note that, among its other beneficial effects such as the breaking of the primary enforced seed-coat dormancy, fire may act to remove any inhibitory organic material from around the seed-store and thus enhance germination (Roux and Middlemiss, 1963; McPherson and Muller, 1969). It is reasonable to suppose that interspecific seed-litter inhibitions could act in the field and, therefore, artificially planted *Virgilia* might, by means of its accompanying leaf litter, act to curb the regeneration of *Acacia* and *Albizia*.

The number of long-lived seed-stores of pest Australian legumes is the most difficult problem pertaining to their control. For instance, in combination with other control measures the planting of *Eragrostis curvula* by the Grahamstown municipality in adjacent regions cleared of *Acacia longifolia* has so far successfully inhibited seed-store regeneration (McDowell, pers. obs.). *Eragrostis curvula* seed was the only species found to be immune to inhibition by cold-water extracts of the closely-related *Acacia cyclops* and *A. saligna* (Jones *et al.*, 1963).

Early seedling growth or vigour has been correlated with seed mass or energy (Salisbury, 1942; Grose and Zimmer, 1958) and thus may have some connection with the initial competitive vigour of the test species. However, *Albizia*, although possessing the greatest seed energy content, lagged behind *Virgilia* both in overall shoot length, root length and biomass increments as well as in competitive success. It could be argued that this results from the early shedding of the apparently non-photosynthetic cotyledons of *Albizia*, whereas the other two species retain their cotyledons as photosynthetic organs throughout. However, *Albizia* appears to have sufficient energy to overtake *Acacia* which possesses a far lower quantity of seed energy than either *Albizia* or *Virgilia*.

Newman (1973) maintains that shoot competition for light is the one obvious factor which can produce a competitive advantage of one species over the other. Results from the replacement series competition experiment tend to support this hypothesis, the increase of competitive inhibition for the three species corresponds with the increase in stem height. This correlation was also found in similar competition experiments involving seedlings of six *Eucalyptus* spp. (Burdon and

Pryor, 1975). Although this inference is valid, it cannot be fully verified unless the roots are isolated from one another during competition (Harper, 1977).

It is important to emphasize that, although the competitive enhancement/inhibition effects were largely significant at the stage of harvesting, the trends do not necessarily represent the final outcome, because the percentage mortality was negligible (never exceeding 15 % for any of the species in any culture). Possible reasons why the present situation does not reflect the final outcome may involve certain characteristics of the autecologies of *Albizia* and *Acacia*. For example, both species can evidently produce greater lengths of root with less energy than *Virgilia*, permitting an increase of nutrient transfer into the shoots, which is vitally important for light competition. In *Albizia* this is reflected by a later-developing, slightly faster growth rate for both shoots and roots. With *Acacia* the initial seed energy shortfall is slightly offset by the retention of photosynthetic seed cotyledons for up to 4 months (Milton, 1980), and also by the fact that no phyllodes had developed during the course of the experiment. If the experiment had been run for a longer period it is possible that the more robust phyllodes would have enhanced the photosynthetic capacity of *Acacia*, thereby increasing the production of its relatively low-energy roots, and hence shifting the competitive advantage to its favour.

However, it could be speculated that if the application of water in the experiment had not been optimal, mortality in the mixed stands relative to the pure might have been higher in the competitively inhibited plants, as the effect of species dominance appears to be most significant in the root biomass. If the latter were reduced in favour of an increase of energy to the shoots, in order to obtain access to the restricted light space, it is possible that the inhibited species might, by comparison with pure stand members, have become more susceptible to drought. In other words, too great a rate of transpiration might occur, relative to the capacity of water-uptake.

Among other environmental factors in the field which could alter the competitive balance between the species are differing moisture and nutrient availabilities of different soils (for example, *Virgilia* could represent a more vigorous competitor when growing at optimal conditions in a rich clay-loam similar to the experimental soil), in which the moisture content ranges from 35 to 50 % of dry mass (Phillips, 1926). However, *Albizia* may develop a competitive advantage over *Virgilia* in a poor, leached soil, as evidenced by its slightly improved performance in the non-nutrient vermiculite. An analogous situation may also apply in more advanced competition stages in which *Albizia* might tolerate lower nutrient levels. If this speculation is correct the addition of low fertilizer concentrations may boost the competitive power of *Virgilia* over that of *Albizia*. Only further experimentation can answer this question.

If one concedes that *Virgilia* occupies a similar niche to that of *Albizia* and *Acacia* what then is the prime reason for the greater geographical distribution of

the two alien species (most obvious in the Cape Peninsula)? This could be due to extensive plantings in the past (Shaunessy, 1980). Present knowledge of the behaviour of invading species also indicates that it is in the phases of germination and seedling establishment that success or failure in extending distribution is most critically determined (Harper, 1969). Superficial field examination of seed and seedling predation of the alien *Albizia/Acacia* relative to *Virgilia* reveals that at least part of the answer for *Virgilia*'s comparative lack of establishment may lie in its greater susceptibility to predation. Phillips (1926) records several agents, in addition to those described, which are destructive to both regenerative and adult stages of *Virgilia*.

If some biological means for curbing the regeneration of *Albizia* and *Acacia* similar to the insect control attempted for *Hakea* spp. (Neser, 1974, 1976) is introduced, it seems reasonable to suggest that interspecific competition by *Virgilia* might, if managed correctly, act as a subsidiary measure for the reclamation of regions infested by *Albizia* and *Acacia*. *Virgilia* has the additional advantage that it acts as a nurse plant to permit the seral establishment of other indigenous trees (Phillips, 1926), which may also play a rôle in the further suppression of *Albizia* and *Acacia*.

CONCLUSIONS

The observation of Harper (1977) that the most appropriate manner in which to detect differences in the ecologies of separate populations (or species) is to grow them together in mixtures has been, directly or indirectly, confirmed in this study. The broad hypothesis that the test legumes occupy similar niches has been verified and in addition several important, although minor, ecological differences have been highlighted by the comparative approach which was adopted in the experimental procedure.

It has been demonstrated that experiments using small samples can yield workable results. These results, analysed selectively, have provided some insight into what is broadly speaking an attempt to channel research directly into solving a pressing and urgent problem—that of controlling or curbing pest-plant encroachment by creating a natural replacement by desirable species (Piemeisel and Carsner, 1951). Thus it is hoped that this article has opened an alternative avenue of approach to the subject of pest-plant control, i.e. the careful manipulation of our own biological resources.

Future research should also involve field trials, along the lines being followed at present by Professor H. B. Rycroft, who is planting experimental plots of *Virgilia* on the *Acacia*-infested mountain slopes at Banhoek Valley, Cape Province. It also may prove of value to investigate other indigenous species that could play a similar out-competing rôle.

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